46. On an Instance of Commensalism between a Hermit Crab and a Polyzoon. By R. Kirkpatrick, F.Z.S., and Dr. J. Metzelaar.

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(Plates I., II.*)

General.—In the year 1906, Mr. F. P. Vermeulen, Ymuiden, Holland, started with a fishery expedition to the West African shores with the object of seeing if the "langusts" of Cape Blanco and its neighbourhood would be worth exploitation. The rich material collected by him was given to the Zoological Society, "Natura Artis Magistra," at Amsterdam. It contains many Hermit Crabs, the commonest of which is *Petrochirus granulimanus* Miers.

The younger specimens of this Crustacean live in small shells of *Turritella brevialis*, *Natica fulminea*, *Nassa miga*, *Terebra senegalensis*, *Aporrhais pes pelecani*, and *Dorsanum politum*. These samples come from Cape Blanco and the large Greyhound Bay ("Baie du Levrier") close by, from depths not exceeding 20 metres. A few specimens were also met with on the Senegal coast.

Now, some of these "youngster" home-shells show a thin incrustation of a Polyzoon, a few layers thick near the orifice and only one or two layers over the rest of the surface (Pl. I. fig. 3).

If we compare the older young and adult pagurids with the former, we notice the said colony has increased very much, resulting in a heavy turnip- or potato-like spheroidal mass, about 6 cm. in diameter (fig. 1), completely involving the original contour of the shell. At one side there is a funnel, about 2 cm. wide externally and filled in by the heavy claw of the *Petrochirus*. A section (fig. 2) shows the gasteropod shell covered entirely by a dense, stony crust of the Polyzoon in numerous layers, amounting to 56. The shell-substance does not appear to have been eaten away as in shells encrusted by *Lepralia edax*. The free margin of the orifice of the larger specimens is made up wholly of Polyzoan layers folded on themselves (fig. 2). On dissection, the calcareous Polyzoan mass appears to be homogeneous, excepting that a few barnacles have been overwhelmed and suffocated. The most sound colonies have a perfectly smooth surface of a deep violet-brown colour in spirit, and they form a typical feature of the fauna of the Cape Blanco coast. But for reasons not yet explained the colony may lose its power of resistance against destructive forces of the environment. Everyone knows the difference between "living" mollusc-shells, so eagerly wished for by conchologists, and the porous, brittle shells, the legal inhabitants of which have been replaced by boring

* For explanation of the Plates, see p. 990.

animals. Exactly the same is the case with our Polyzoon. The simple colonies from one station have all changed into microcosms of sessile invertebrate life. Large specimens of *Lithodomus* easily lodge in the thick, limestone-like wall without touching their motor-pagurid. There are the big colonies of a compound ascidian (*Distomus* sp.), purple barnacles, bushy hydroids upon the Polyzoan wall (Pl. II., fig. 14). Although very interesting from an œcological point of view, we shall not describe these compound colonies as they do not show *constant* features, the original Paguro-Polyzoan association having lost its exclusive character. Meanwhile it illustrates the fact that mobility of substratum is favourable to diverse forms of sessile animal life.

By the way, we may notice one rather striking fact. Although the weight of its limestone house with weeded roof *must* become a nuisance to the Hermit, however powerful it may be, let us mention one point in favour of its security. In one of the hydroid tufts a spawning *Sepia* has glued several eggs. So this professional crab-eater remained unconscious of the close proximity of its prey, and the most critical sceptic must admit that this argument, taken from nature itself, is stronger than any aquarium experiment as to the efficiency of this pagurine mode of life.

As a counterpart to this, we may add that remains of *Eupagurus bernhardus* are often found in the stomachs of Cod from moderate depths in the North Sea.

Description of the Polyzoon, based upon $4\frac{1}{2}$ adult and 3 young samples sent to the Natural History Museum, London.

A glance with a good lens at once shows the Polyzoon to be a member of the great Membraniporidan group. The surface of the zoarium is covered with a membrane, which can be peeled off. The zoœcia are arranged in straight, longitudinal rows, the latter every now and then bifurcating. The zoœcia are not abreast transversely, but in quincunx. A five of diamonds in cards, with the pips uniformly enlarged till they nearly meet, would illustrate the plan.

The zoœcia (Pl. I. figs. 4, 5, 6) are oval, and on an average 0·6 mm. long and 0·3 mm. wide in the middle. The margins of the zoœcia in well-preserved material are mapped out by dark brown membranous or chitinous lines. Busk calls attention to similar "brown lines" in his description of *Membranipora denticulata* Busk.

The calcareous margin is strongly granulated, and slopes inwards and downwards to a finely serrated edge bordering the oval opesia.

At the proximal or basal end of each zoœcium and immediately below the opesia there are two triangular, flattened, hollow tubercles, separate in the young stage, but joined into a single rectangular block in older zoœcia (figs. 4, 5, 6). The brown line separately surrounds each triangular tubercle and also each rectangular block.

The ectocyst in the surface layer of zoœcia is membranous. The operculum is 0·06 mm. long and 0·08 mm. wide, and with the rim thickened, especially laterally. In the older layers of zoœcia the opesia is filled in, not by membrane, but by a thick punctate, calcareous plate, convex on its lower surface, and further, the zoœcial walls become thickened, so that the zoarium becomes hard and stony. Rosette-plates multiporal: usually four in each lateral wall; two, occasionally several, in the distal wall.

There are no avicularia and no oœcia.

There need be no hesitation in assigning the Polyzoon to the genus *Conopeum* Gray * (genotype: *lacroixii* Audouin †) as amended by Norman ‡ and Canu & Bassler §.

But the determination of the species has been a more difficult problem. One high authority, to whom the material had been sent, identified the species as *Membranipora tehuelcha* d'Orbigny. We were at first inclined to regard the species as a variety of *Conopeum lacroixii* Audouin, but finally we have come to the conclusion that the species is new to science. We propose to call it Conopeum commensale, sp. n.

The distinguishing characters of the new species are: the thick zoœcial walls, the thick calcareous opesial plate, and the dense stony multilaminate zoarium. Neither the well-known British *Con. lacroixii*, as described by Busk and Hincks, nor the Mediterranean form, as described and figured by Audouin and Savigny, have any of these characters. If in the British form of *C. lacroixii* occasionally one layer grows over another, there are no calcareous opesial in-fillings; and, moreover, "the triangular hollows on each side above the aperture" (Hincks, Brit. Mar. Pol. p. 130) have each an opening, covered by membrane, and do not fuse into a single rectangular block. This fusion does, however, take place occasionally in the typical form, figured in the 'Description de l'Egypte,' pl. x. fig. 9. The new species differs widely from *M. tehuelcha* d'Orbigny. We had the good fortune to find numerous specimens encrusting the alga *Macrocystis pyrifera* from the Straits of Magellan and from Valparaiso and the coasts of the Tehuelchan region (the T. being a great tribe of Patagonian Indians). The zoœcia (fig. 12) are very different in shape and character, being thin-walled, elongated, rectangular boxes with sharp edges; and the triangular knob and fused rectangular structures of *C. commensale* Kirkpatrick & Metzelaar are replaced by a pair of rather long, blunt calcareo-chitinous "spines." *M. tehuelcha*, in our opinion, is little

* Gray, List of British Animals.—Part I. Radiated Animals, pp. 108, 146 (1848).

† It is held by several authorities that Audouin's "*Lacroixii*" is a synonym of *Millepora reticulum* Linné.

‡ Norman, Nat. Hist. East Finmark. Ann. & Mag. Nat. Hist. (7) xi. p. 586 (1903).

§ Canu & Bassler, North American Early Tertiary Bryozoa. U.S. Nat. Mus Bull. 106, text pp. 84, 86 (1920).

other than a South American representative of *Membranipora membranacea* L.

The study of the triangular objects in *C. lacroixii* Audouin and in the early stages of *C. commensale* Kirkpatrick & Metzelaar has, we think, thrown an interesting light on certain structures found in widely separate families and genera. The precise nature of the "triangular hollows" * in *C. lacroixii* is not definitely known, but the view that they are diminutive zoœcia, aborted owing to exigencies of space, appears to us a reasonable one. Cramped zoœcia are often found among the rows and layers of ordinary zoœcia. The openings of the inter-zoœcial triangular hollows of *C. lacroixii* have granulated margins, precisely comparable with the edges of ordinary zoœcia, and under a high power the whole structure is fairly similar in aspect to an ordinary zoœcial box somewhat distorted.

In *C. commensale* the triangles have a calcareous roof, and are bounded each by a separate brown line. Where the triangles are fused into one rectangular block, there is only one line round the block. A fundamental and—with the exception of *Loxosoma*—universal character of the Polyzoa is that of budding so as to form colonies. Limitation of space must lead to a struggle among the buds, with partial or complete suppression of some.

It would appear that in *C. lacroixii* each zoœcium gives off three distal buds, the lateral ones being almost, but not wholly, suppressed.

A careful examination of many species of Cheilostomes has convinced us that the paired spaces, knobs, tubercles, and spines so commonly present are all comparable with the "triangular hollows" of *C. lacroixii*, and that they are modified zoœcial buds † taking on strange shapes and functions. In *Membranipora membranacea* L., for instance, triangular spaces will be found at or near the growing edges of the zoarium; in older cells the "hollows" (really inter-zoœcial boxes) grow up into long spines or tubercles, as if, owing to the limited basal area, they took to building skyscrapers.

In *M. tehuelcha* d'Orbigny (fig. 12) the same event has happened. Here the tops of the spines are often membranous, recalling the membranes over the openings of the triangles in *C. lacroixii*. That this interpretation is not a mere fancy, is shown by the resemblance of the early stages of the spines near the growing edges of colonies to the triangular areas in *C. lacroixii*.

In *M. tuberculata* Bosc, so abundant on Gulf weed, the

* Hincks, 'British Marine Polyzoa,' p. 130.

† *Cf.* the "origellæ" of Jullien, "des bourgeons charnus, développés sur l'endocyste,' which can reproduce zoœcia, avicularia, etc. (Bull. Soc. Zool. France, xi. p. 607, 1886). Later, "jonctures," which produce zoœcia, are distinguished from "origelles évolutives," which form avicularia, spines, etc. (Jullien & Calvet, Bryozoaires 'Hirondelle,' 1903, p. 18).

tubercles, at first separate, may join together to form single blocks as in *C. commensale*; a remarkable example of the former species is shown in fig. 11, where the blocks have developed so enormously as almost to obliterate the opesia.

In descriptions, the triangular hollows, spines, tubercles, etc. are usually associated with the distal or oral end of the zoœcium, but they should perhaps rather be associated with the proximal or basal part of a zoœcium. On the triple-bud hypothesis it is certainly more rational to associate the three buds, no matter what their subsequent history and disguise might be; and further, the knobs, spines, etc. are often clearly seated on the front of the basal end of a zoœcium. Take, for example, the little knobs on the zoœcia of *Membranipora savartii* Audouin, shown on the base of each cell in Savigny's figure ('Description de l'Egypte,' Atlas, pl. x. fig. 10) *.

In *Thairopora armata* MacGillivray (fig. 13) the two club-shaped tubercles are situated one on each side of the oral orifice of a zoœcium, and, it must be admitted, a little imagination is required to realize that even here the tubercles should perhaps be associated with the proximal end of the following zoœcium. One might assume that the two lateral buds had been given off at right angles to the central one, instead of at a forward-opening acute angle.

The avicularian cell in this species appears beautifully to confirm the theory of homology of tubercles and triangular boxes; for here, in place of tubercles, and on each side of and above the avicularian opening, there is a triangular box with a clear space in the roof (fig. 13).

Possibly the quincuncial plan of growth so common in Cheilostome Polyzoa may be due to adaptation to limited space. Zoœcia giving off three buds at the distal end would not be well able to grow abreast; accordingly the buds (and their adult equivalents) often alternate transversely.

The fusion of two lateral hollow knobs into one rectangular hollow box in *C. commensale* may be connected in some way with reproduction, for in decalcified specimens there can usually be seen a brown body or developing new polypide in the zoœcial cavities adjacent to these boxes.

Discussion.—On two points our description of the new species is open to adverse criticism. Firstly, we attribute specific value to zoarial characters. During an early period of the study of Polyzoa, zoarial characters alone were considered, most of the encrusting and branching calcareous Cheilostomes being relegated to *Lepralia* and *Eschara* respectively. Later, zoœcial characters became all-important, the zoarial ones being entirely put aside. At the present time the tendency is to take all characters into

* There is rarely any trace of the knobs in the specimens of this species from tropical seas or from Japan.

consideration, judging each case on its own merits. A good example of the specific value of zoarial characters is afforded by *Lepralia bifurcata* Waters, found in deep water off Capri. Here we have a typical *Lepralia*, but one that always grows in a very definite, peculiar, and characteristic way, viz. as a bifurcating colony with two little wings. No matter how closely the characters of the individual zoœcia resemble those of some particular encrusting *Lepralia*, it would be difficult to regard the bifurcating colony as a mere variety or variation of the encrusting one. Similarly, we regard the dense, stony, multilaminate Polyzoon from Cape Blanco as specifically distinct from the slender, thinly encrusting *C. lacroixii*, *the modified character*—if we may adopt the neo-Lamarckian line of thought—*having perhaps resulted from epœcal*, e. g. *well-fed life.*

Biology.—Again, the adoption of the name "*commensale*" might be considered a doubtful proceeding. We think the name, however, to be convenient, not only from the point of view of easy identification, but justifiable as indicating the real relationship existing between the Polyzoon and the Crustacean. There is evidently no question of true symbiosis or mutualism *sensu strictiore*, if we define that as "legal relation between two different organisms," principally, because *Petrochirus granulimanus* can live and thrive without *C. commensale*. Leaving the young Crustacea aside, we find the adults associated with the sponge *Suberites domuncula*, the compound zoantharian *Corticifera lutea*, and the Polyzoon *Lepralia edax*.

But the reverse does not seem to be the case. Polyzoa growing on the hydroids and corals of the Vermeulen-expedition did not include *C. commensale* among them. Nor did we notice it upon living molluscs from the same localities. *Possibly* the Polyzoon could survive for a time on an untenanted shell with much diminished vitality, but so far there is no evidence on this point, although we must take into consideration that the West African material has been collected by one who was not a zoologist.

According to Prof. Calvet, any smooth surface is suitable to the Membraniporæ, and "associations of hermit-crabs and Polyzoa are common enough." Even so, we never saw them before in such a definite non-accidental mode and shape. The Paguro-Polyzoan association described here appears to be a *definite* and not an accidental one, the Crustacean and Polyzoon being more to each other than casual messmates; for it is certain they derive special advantages from each other's presence.

Hermit Crabs are widely distributed all over the world, and are notorious for their militant and aggressive nature. Ensconced in their shells they are veritable tankers, spreading dismay among their helpless victims. Every now and again, when the soldier has to leave his fortress, his softened body is exposed to danger. But frequently some other organism (Sponge, Cœlenterate or, more rarely, Polyzoon) adapts itself to the shell, and gradually acquires certain special characters. The encrusting

animal forms an extra panoply, not merely thicker, but more extended, especially around the shell orifice, thereby generally ensuring a longer tenancy to the Crustacean. This feature of extended growth is illustrated in fig. 2, where the opening of the fortress is seen to be formed, not of shell, but of infolded layers of the Polyzoon. Again, the Polyzoon obviously benefits; for it is in alliance with a vigorous and successful marauder, and although sedentary by nature, is continually being carried to new and rich pastures.

Accordingly, the large size of the new species is not surprising.

We return now, after this economic excursion, to the peculiarity of the association described. Against critics who deny the non-accidental nature of it, we draw attention to one main point. Setting apart those favourite Pagurine mates: *Suberites* and the epœcal Zoantharians, there remains the fact that a "special seat" is reserved to *Conopeum commensale* among the hosts of sessile epœcal animals, *ready to populate every available spot* in the tepid tropical coast-waters. In a very short lapse of time a typical complex is formed. This follows from the fact that among the many home-shells of adult *Petr. granulimanus* only one was found naked, obviously inhabited only a short time before it was caught; intermediate gradations to full-grown adult colonies are wanting. Now, what is the reason that among so many rivals the tiny Polyzoon regularly wins the battle? We have seen that the other candidates may win the second round if the Hermit migrates to a spot unfit for its Polyzoan comrade to live in. In the struggle for life the champion is slain at last. *Now* at last a fair chance is given to everybody; here you have Accident playing its part, and the result . . . . a chaotic conglomerate of sessile marine life (fig. 14).

Since the time of Darwin, Law has taken the place of Accident in biological science.

Our case is in some respects comparable to the well-known association of *Eupagurus bernhardus* and *Hydractinia echinata*. In this case the Pagurid inhabits the whole "littoral" region up to a depth of 270 metres, but *Hydractinia echinata* is a coastal form which does not follow the adolescent *Eupagurus* to depths exceeding those of the centre of the North Sea. At the lower limit of its occurrence the *Hydractinia* is often replaced by *Alcyonidium gelatinosum*. Now, although *Hydractinia echinata* has been found in a few instances without its mate *Eupagurus bernhardus*, is there anybody who will seriously contest the particular relation between these two organisms? Cf. *Eupag. pubescens*, which occur in the North Sea as a rule, associated with *Suberites ficus*, but exceptionally with *Zoanthus* sp.

So far as we know, the present case has not yet been described. It is a remarkable fact that Chevreux and Bouvier, among the rich material of the 'Melita,' described 17 species of Pagurids (Mém. Soc. Zool. France, v. 1892), but only noticed "coquille

recouverte de bryozoaires" in the case of *Petrochirus granulimanus*. The "bryozoaires" have probably been *Con. commensale*, but they were not examined.

In the volume dealing with the results of the inquiries of the 'Travailleur' and 'Talisman' immense numbers of Polyzoa are mentioned, but no reference to the present case.

Summary and Conclusion.—The present Polyzoon from the Cape Blanco region is a new species, viz. *Conopeum commensale* Kirkpatrick & Metzelaar. It is most nearly related to *C. lacroixii* Audouin.

The paired "triangular spaces," paired knobs, tubercles, or spines so commonly present in many species of Cheilostome Polyzoa are probably aborted zoœcial buds, more or less suppressed or modified owing to lack of space for free growth.

The association with the Crustacean *Petrochirus granulimanus* is a definite, not an accidental one, being a case of commensalism in the sense of Van Beneden.

EXPLANATION OF THE PLATES.

(The figures to be examined through a hand-lens.)

Plate I.

Fig. 1. Gasteropod shell inhabited by *Petrochirus granulimanus* Miers, completely encrusted by the Polyzoon *Conopeum commensale* Kirkpatrick & Metzelaar from Cape Blanco. Nat. size.

2. A shell and Polyzoan crust cut in half. Nat. size.

3. *Turritella* shells inhabited by Hermit Crab, and each encrusted by young colony of *Conopeum commensale*: from Senegal. Nat. size.

4. *Conopeum commensale*. × 20.

5 & 6. The same from another specimen, showing at the first separate triangular tubercles and the single rectangular blocks. × 20.

7. An older layer of zoœcia broken into and viewed from the inferior or dorsal aspect, showing calcareous infillings of the opesiæ. × 20.

8. *Conopeum lacroixii*, showing the two separate triangular "spaces" (boxes) at the base of each zoœcium. × 20.

9. *Conopeum commensale*. Transparent vertical section, showing layers. × 3½. (*Cf.* fig. 2.)

10. *Conopeum lacroixii* Audouin, showing separate triangular hollows: specimen from Dovercourt, England. × 20.

11. *Membranipora tuberculata* Bosc, encrusting two sides of alga from Algoa Bay; showing remarkable blocks at the margin of colony, also ordinary paired tubercles. × 20.

12. *Membranipora tehuelcha* d'Orbigny on *Macrocystis pyrifera* from South America; showing the two spine-like tubercles to each zoœcium.

13. *Thairopora armata* MacGillivray, showing zoœcia with paired boss-like tubercles and an avicularian cell with triangular hollow boxes above mandible. × 20.

N.B.—There is an avicularium with sharply-defined triangular mandible about 8 mm. above the middle of the lower border of the picture. The mandible and the triangular boxes above it have a frog's-face-like aspect. In the ordinary zoœcia the pairs of white boss-like tubercles replace the triangular "hollows" or boxes. A lens is necessary.

Plate II.

Fig. 14. Bulbous specimen secondarily overgrown with hydroid, etc.